

# Host-specific demography of *Utetes anastrephae* (Hymenoptera, Braconidae), a native parasitoid of *Anastrepha* spp. fruit flies (Diptera, Tephritidae)

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## Abstract

The braconid *Utetes anastrephae* (Viereck, 1913) (Hymenoptera: Braconidae) is a larva-pupal parasitoid of fruit flies of the genus *Anastrepha* Schiner, commonly associated with *Anastrepha obliqua* (Macquart, 1835) (Diptera: Tephritidae), the most important pest of mango (*Mangifera indica* L., 1753) in Mexico. This parasitoid was established in a laboratory colony using larvae of *Anastrepha ludens* (Loew, 1873) as host. Here we describe a demographic study to compare the reproductive and population parameters of this parasitoid reared on *A. obliqua* and *A. ludens* under laboratory conditions. Two *U. anastrephae* cohorts of 30 individual pairs each were set up, one was reared on *A. obliqua* larvae and the other one on *A. ludens*. Every day, 30 third instar larvae of each host species were exposed to an adult pair through the lifespan of the female. Daily mortality and fecundity were recorded. Life tables were constructed and sex ratios, parasitism rates, survival, reproductive and population parameters were estimated. Higher survival of *U. anastrephae* females was observed in females from *A. obliqua* (mean live expectancy of 22.4 days), but higher fecundity and parasitism occurred in females from *A. ludens* (net fecundity of 62.61 daughters/female and 16.72% parasitism rate). The intrinsic rate of increase ( $r = 0.128$  and  $r = 0.134$  for *A. obliqua* and *A. ludens* respectively), mean generation time (27.88 and 28.30 days) and population doubling time (5.42 and 5.16 days) were similar in both cohorts, as well as the sex ratio (73 and 69% of females). These results suggest that *A. ludens* as host increase the production rates; however, any one of these two species could be used as host for mass rearing purposes.



**Keywords**

biocontrol, fecundity, intrinsic rate of increase, life table, mass rearing, parasitism, survival

**Introduction**

The use of native parasitoids for the management of *Anastrepha* fruit flies has been a subject of discussion, since these species would be used in an environment where fruit flies generally have a higher rate of natural increase (Vargas et al. 2002; Aluja et al. 2009). However, given the good results obtained with augmentative releases of *Diachasmimorpha longicaudata* (Ashmead, 1905) in different environments (e.g., Montoya et al. 2000; Montoya et al. 2007; Montoya et al. 2016; Cancino et al. 2019a), the potential for native species for the control of *Anastrepha* fruit flies is worth to explore.

*Utetes anastrephae* (Viereck, 1913) (Hymenoptera: Braconidae) is a koinobiont, solitary endoparasitoid (Ovruski et al. 2000) native to the Neotropics that parasitizes larva-pupa of fruit flies. It is found parasitizing *Anastrepha obliqua* (Macquart, 1835) (Diptera: Tephritidae) feeding upon *Spondias* spp. (Anacardiaceae), and in minor frequency in other species such as *Anastrepha alveata* Stone, 1942 and *Anastrepha fraterculus* (Wiedemann, 1830) (Aluja et al. 1990; Hernández-Ortíz et al. 1994; López et al. 1999). This parasitoid competes successfully with other native braconid parasitoid species, such as *Doryctobracon areolatus* (Szépligeti, 1911), *Doryctobracon crawfordi* (Viereck, 1911), and *Opius hirtus* Fischer, 1963; it even competes with the introduced *D. longicaudata*, showing a remarkable capacity for conspecific discrimination and heterospecific intrinsic competition in previously parasitized larvae (Aluja et al. 2013; Ayala et al. 2018; Murillo et al. 2018).

The use of a parasitoid species for augmentative biological control applications requires the development of methods for mass production of good quality individuals. One essential element is the selection of an adequate host species (Eitam et al. 2003; Cancino et al. 2009). Although *A. ludens* is not considered a preferred host for *U. anastrephae*, it can be used as an alternative host because it is a species relatively easy to rear, being a high-quality host that is currently used to produce massively *D. longicaudata* (Orozco-Dávila et al. 2017; Cancino et al. 2020). Under laboratory conditions *U. anastrephae* successfully parasitizes 5–8 days old *A. obliqua* larvae (Poncio et al. 2018) and 7–8 days old *A. ludens* larvae (Aluja et al. 2009; Cancino et al. 2009).

Knowledge of the demography of parasitoids, in addition to allowing a better understanding of their biology, allows us to compare the effect of different hosts and make mass rearing more efficient (Bellows et al. 1992; Carey and Roach 2020; Ganjisaffar and Perring 2020). For example, the intrinsic rate of natural increase ( $r$ ) is a population parameter described as the potential growth of a population (Jervis and Copland 1996) and can be used as an indicator of the capacity of a parasitoid species to suppress or regulate the target pest population (Vargas et al. 2002; Stark et al. 2004). This parameter combines both the survival and reproduction of a population and allows



comparison among different species of parasitoids or when species are evaluated under different environmental conditions (Núñez-Campero et al. 2014; Gonçalves et al. 2018; Fernandes et al. 2021).

Our previous trials, trying to establish a colony of *U. anastrephae* using *A. obliqua* larvae as host, were unsuccessful, despite being considered its natural host. Here, we used a strain of *U. anastrephae* reared on *A. ludens* larvae as host, applying the concept of factitious host used for *Trichogramma* spp. mass rearing (Iranipour et al. 2010; Gowda et al. 2021). Our hypothesis was that the demographic parameters of *U. anastrephae* would be affected by the host species used for the development of their offspring. Therefore, our aim was to determine the effect of two different hosts, *A. obliqua* (the preferred host in nature) and *A. ludens* (the host used in laboratory rearing), on the survival, reproductive and population parameters of *U. anastrephae*. Our results improved our understanding of the performance of *U. anastrephae* reared on both host species and indicate that both can be used for mass rearing it as a biocontrol agent of *Anastrepha* fruit flies.

## Materials and methods

### Biological material

The study was carried out at the Laboratory of Biological Control, of the Programa Moscafrut (SENASICA-SADER) in Metapa de Domínguez, Chiapas, Mexico. *Utetes anastrephae* specimens were obtained from a laboratory colony maintained using *A. ludens* larvae as hosts. This colony was established with specimens of *U. anastrephae* emerged from larvae of *A. obliqua* developed in tropical plum trees (*Spondias mombin* L.). After three unsuccessful attempts using *A. obliqua* as host, we decided to use *A. ludens* as alternative host. This strategy was successful in terms of colonization and the current colony has  $\approx 250$  generations under laboratory mass rearing conditions. The larvae of both *A. ludens* and *A. obliqua* were obtained from the mass reared colonies maintained at the Moscafrut facility (Orozco-Dávila et al. 2017). All experiments were carried out under laboratory conditions at  $26 \pm 0.5$  °C,  $70 \pm 10\%$  relative humidity, and a 12:12 h L:D photoperiod.

### Oviposition period, parasitism rate and adults sex ratio using two species of host larvae

Two cohorts of *U. anastrephae* of 30 pairs (♀, ♂) each were set up. Individual pairs of newly emerged adults were placed in  $25 \times 11 \times 13$  cm plastic cages. They were provided with water and honey throughout the experiment. One cohort was exposed to *A. obliqua* and the other one to *A. ludens*. Each pair was daily provided with 30 larvae of the corresponding species along the lifespan of each female. The larvae were exposed in parasitization units consisting in 5 cm diameter  $\times$  0.2 cm height Petri dish bottoms,



mixed with larval diet, and covered with tricot fabric clothe fastened with an elastic band. The surface of the parasitizing unit was smeared with ripe guava pulp to attract the parasitoids.

Parasitization units were exposed 4 h every day. Then the larvae with diet were placed in 6 cm diameter × 4 cm height plastic containers. Three days later the larvae were carefully sorted out from the diet with entomological forceps and returned to the same container but now with humid vermiculite as a pupation substrate. The pupae were maintained in humid vermiculite for 14 days at  $26 \pm 0.5$  °C and 60–80% RH. Subsequently, the pupae were removed from the vermiculite and kept in these same conditions until emergence.

The number of dead parasitoids and their sex was recorded daily to estimate sex-specific survival. The number of flies and parasitoids emerged by sex were also recorded every day. Pupae that did not emerge were dissected to investigate the presence of parasitoids or flies. The oviposition period was determined based on the emergence of parasitoids per day. The percentage of parasitism was obtained by dividing the number of emerged parasitoids by the number of exposed larvae, multiplied by 100, as well as the percentage of accumulated parasitism (daily sum of parasitism). The sex ratio of the parasitoids was estimated by dividing the number of females by the sum of females and males and was expressed as the proportion of females.

## Life tables and reproductive and population demographic parameters

To know the survival of the immature stages, 400 larvae of each host species were exposed to two separate groups of 30 couples of five-day old *U. anastrephae* adults; from each host species 20 subsamples of 20 larvae were obtained, and each subsample was dissected daily to know the number of immatures. For life table construction we used the mean egg to adult developmental time and percent survival for each host species.

With the mortality and fecundity data, the corresponding life tables were elaborated, following methods described by Carey (1993), and Carey and Roach (2020). Survival curves were estimated with the proportion of live females per day ( $l_x$ ), that is the number of live females at age  $x$  between the original number of the cohort ( $l_x = N_x / N_0$ ).

In addition, the following reproductive parameters were estimated: gross and net fecundity rates, mean daily offspring production, and mean age for gross and net fecundity. The population demographic parameters were net reproductive rate ( $R_0$ ), intrinsic rate of increase ( $r$ ) using Newton's method based on the formula  $r_1 = r_0 - f(r)/f'(r)$ , finite rate of increase ( $\lambda$ ), mean generation time ( $T$ ), and doubling time ( $DT$ ).

## Data analysis

The experimental design was completely randomized with two treatments (hosts) and 30 replicates, considering each pair of parasitoids as an experimental unit. The data were tested for normality by means of Anderson-Darling test, and for homogeneity of vari-



ances with the Bartlett and Fligner-Policello tests. The pre-oviposition and reproductive periods were compared by means of t-student and Mann-Whitney test, respectively.

Sex ratio and percent parasitism were analysed using a generalized lineal model (GLM) with quasibinomial response, whereas fecundity (offspring per female) was a GLM with negative binomial response. The link-log function was used in each model and a likelihood ratio test was applied to test for the effect of the treatments. Survival curves for females and males were compared using the Log-rank test. A significance level of .05 was used for all statistical tests. All analyses were carried out using the statistical software R v4.0.5 (R Development Core Team 2021).

## Results

### Immatures developmental time and survival

The mean developmental time from egg to adult was 19 days for both host species. Survival of immatures was 68.37% in *A. ludens* and 57.5% in *A. obliqua*. These data were used to construct the life tables and estimation of demographic parameters.

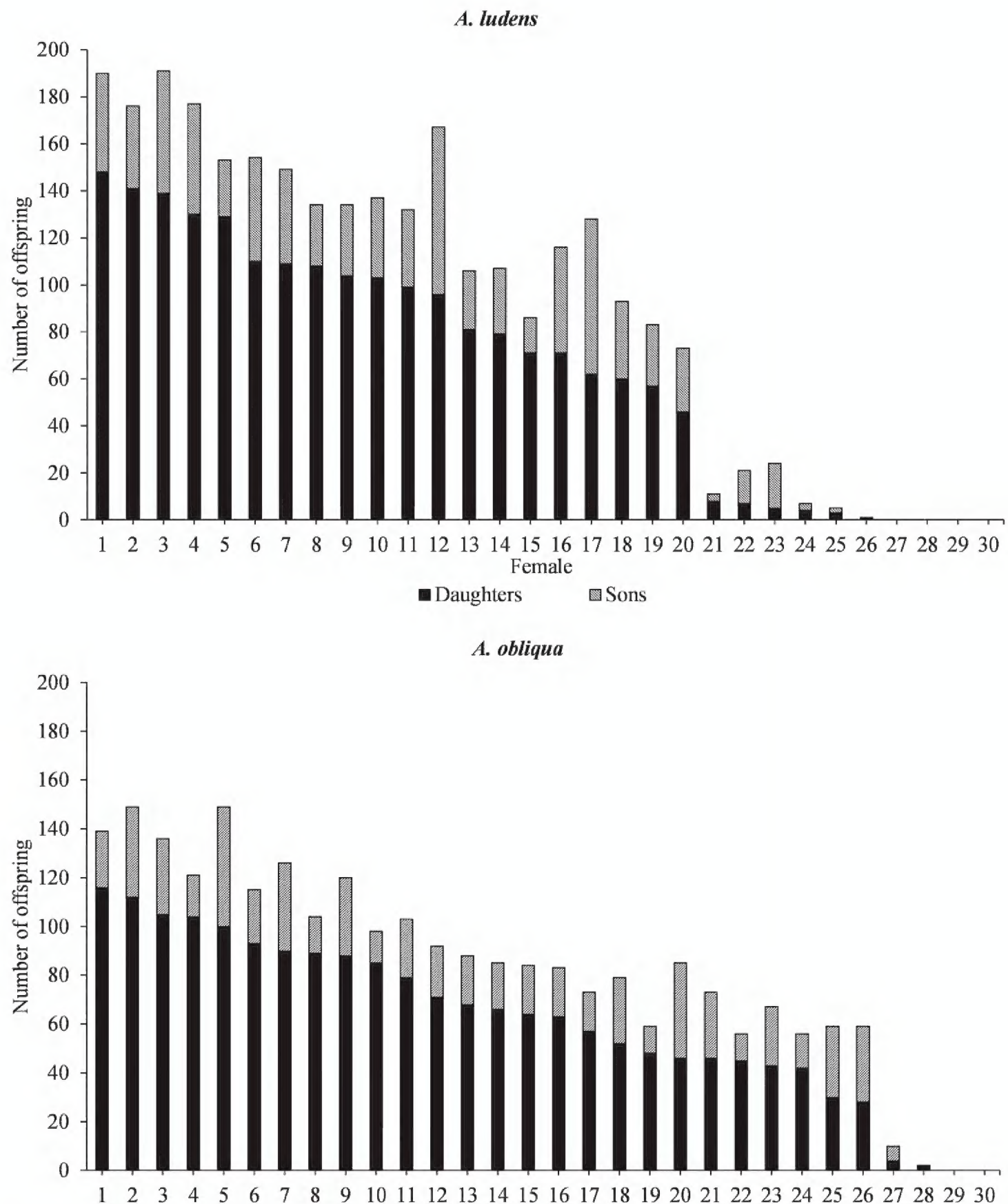
### Oviposition period, parasitism, and sex ratios

The onset of oviposition occurred from the first day of female adult life (first 24 h) for both cohorts. The average female matured on the third day, and it ranged from 1 to 11 days in *A. obliqua* and from 1 to 13 days in *A. ludens*; the pre-oviposition period did not show significant differences ( $W = 368$ ,  $p = .9506$ ) between species. Within the reproductive period, the cohort exposed to *A. obliqua* lasted on average ( $\pm$  SD)  $13.5 \pm 4.99$  days with a range of 1 to 21 days, while the cohort exposed to *A. ludens* lasted  $11.5 \pm 6.11$  days with a range of 1 to 22 days. The difference in the reproductive period of both treatments was not significant ( $t(2) = -1.2899$ ,  $p = .2028$ ).

The percentage of days in which females produced at least one offspring was 65.7% and 86.1% for *A. obliqua* and *A. ludens*, respectively. This means that the cohort parasitizing *A. ludens* larvae produced more offspring in a shorter time. Fecundity (offspring per female) was significantly higher in females from *A. ludens* ( $\chi^2(1) = 15.551$ ,  $p < .001$ ). The maximum number of offspring per female was 191 with a mean ( $\pm$  SD) of  $91.83 \pm 67.77$  individuals per female. For those exposed to *A. obliqua* larvae, the maximum offspring per female was 149 with a mean of  $82.33 \pm 41.87$  individuals (Fig. 1).

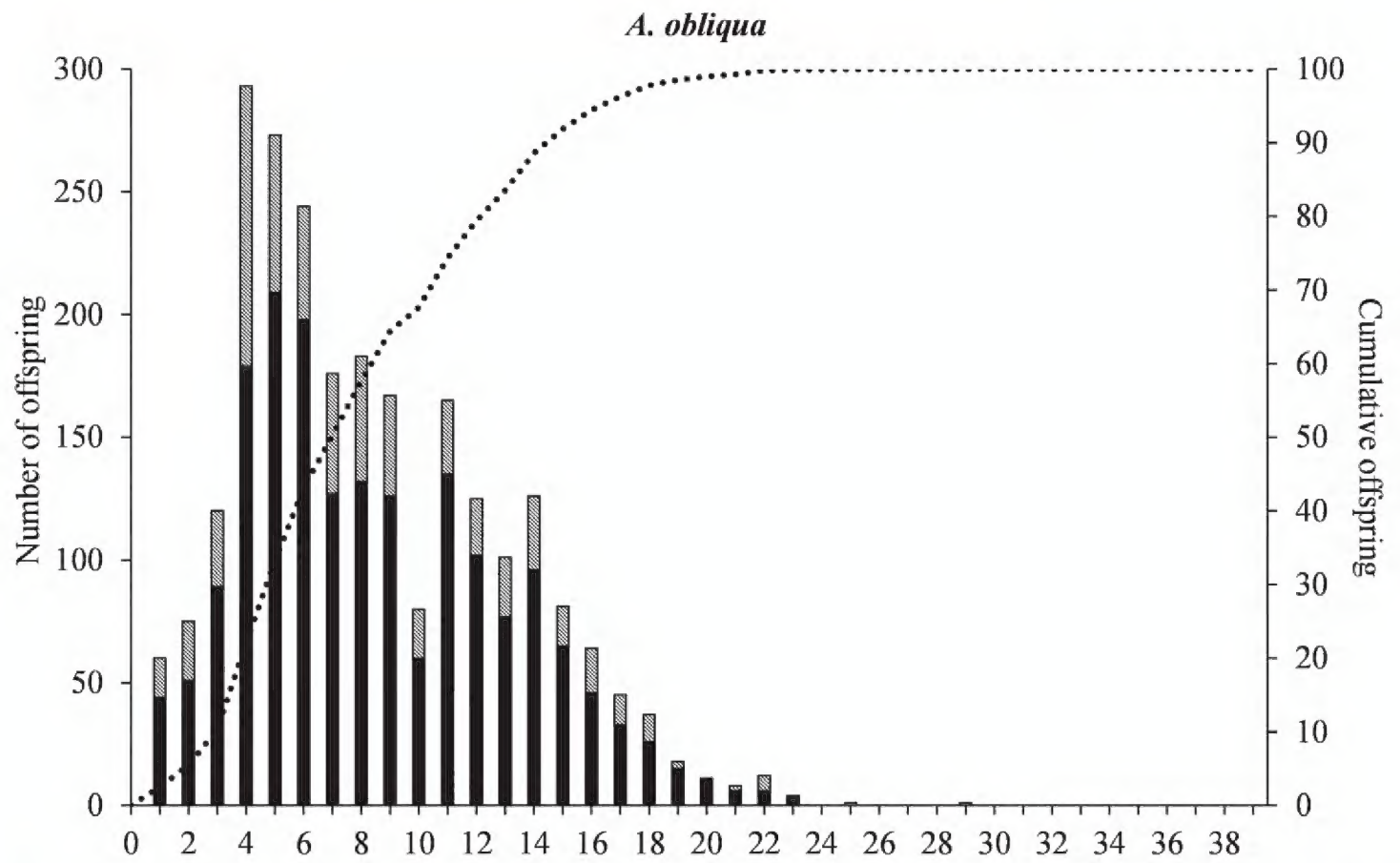
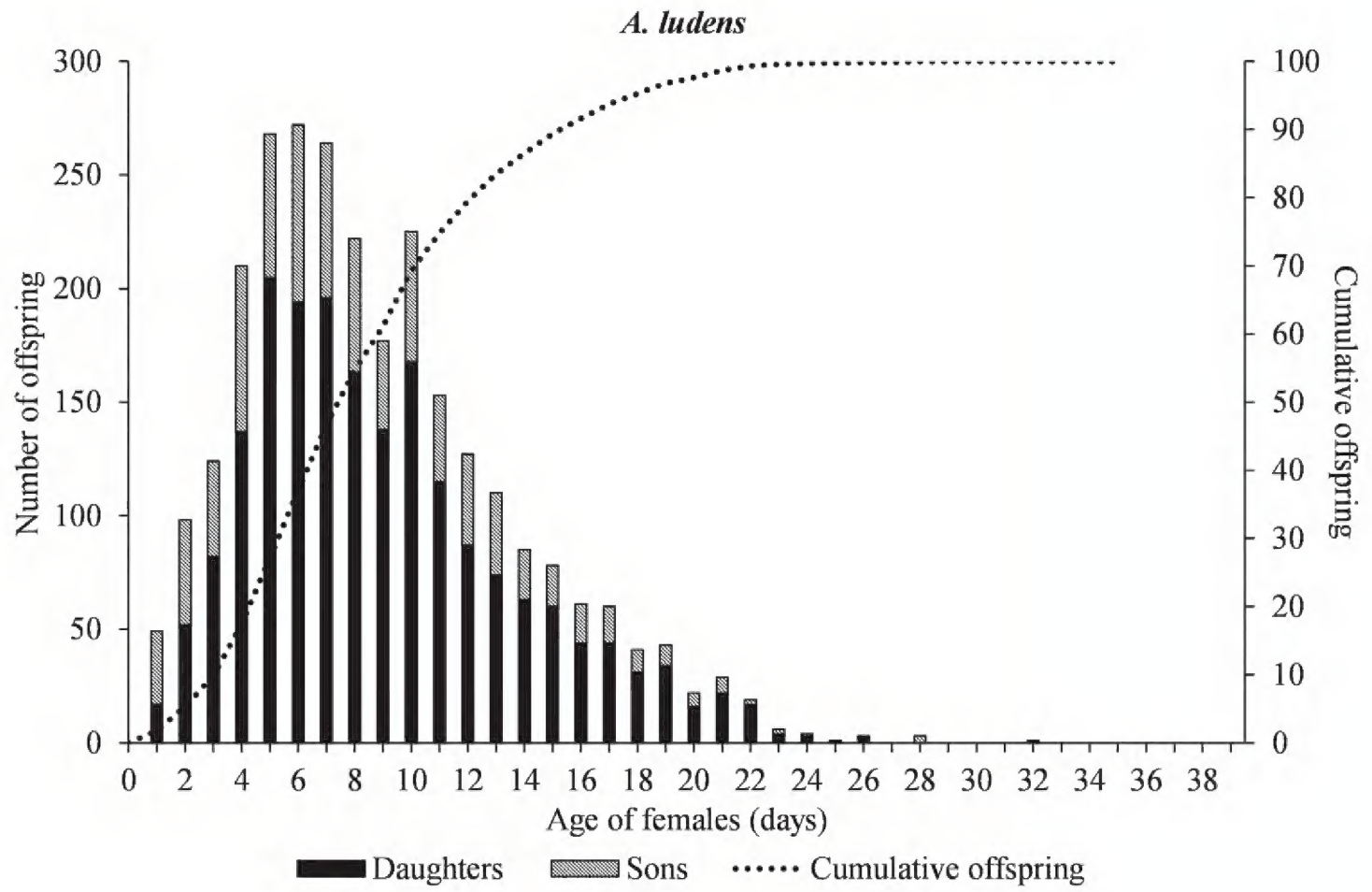
The cohort using *A. obliqua* larvae as a host reached its maximum reproductive peak between four and six days, and by day seven 1241 offspring (50.24%) had been produced. In the case of females that parasitized *A. ludens*, the reproductive peak occurred between five and seven days of age, and by day eight they had produced 54% (1507 individuals) of their total offspring (Fig. 2).





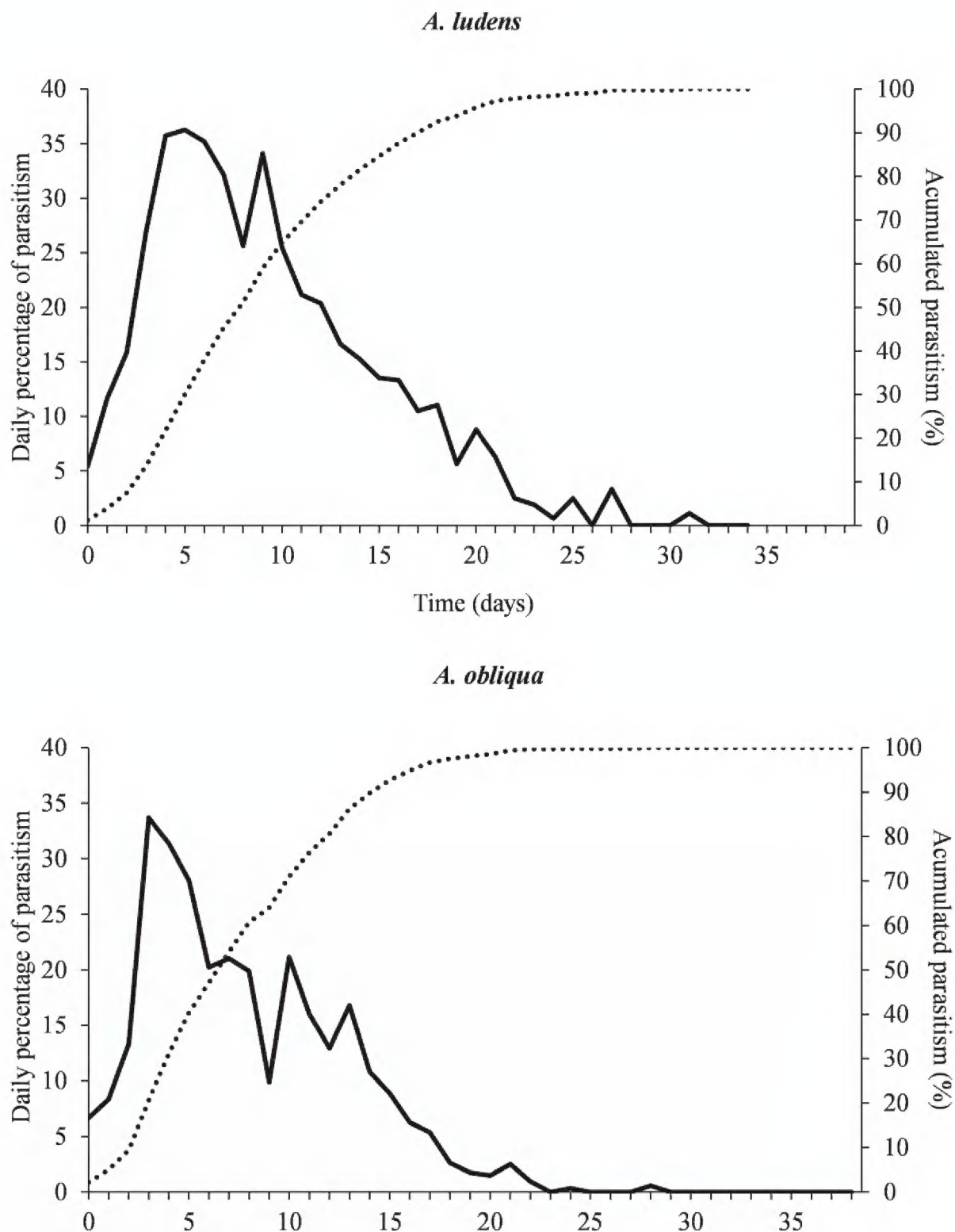
**Figure 1.** Total offspring and sex ratio produced by each female, in both cohorts studied.

Average percentage ( $\pm$  SD) of total parasitism was higher ( $\chi^2(1) = 4.4137$ ,  $p = .0357$ ) in *A. ludens* larvae ( $16.72 \pm 11.56\%$ ), than in *A. obliqua* ( $13.04 \pm 9.69\%$ , Fig. 3). Offspring sex ratio was biased towards females (around 70%) ( $\chi^2(1) = 0.98385$ ,  $p = .3213$ ) and this was observed through the whole females life span in both species ( $\chi^2(1) = 0.00014$ ,  $p = .9904$ ). In *A. obliqua* a proportion ( $\pm$  SD) of  $0.73 \pm 0.13$  females was observed. In *A. ludens* it was  $0.69 \pm 0.16$ .



**Figure 2.** Daily offspring and sex ratio of *U. anastrephae* emerged from *A. obliqua* and *A. ludens* larvae as hosts and their respective cumulative frequency.





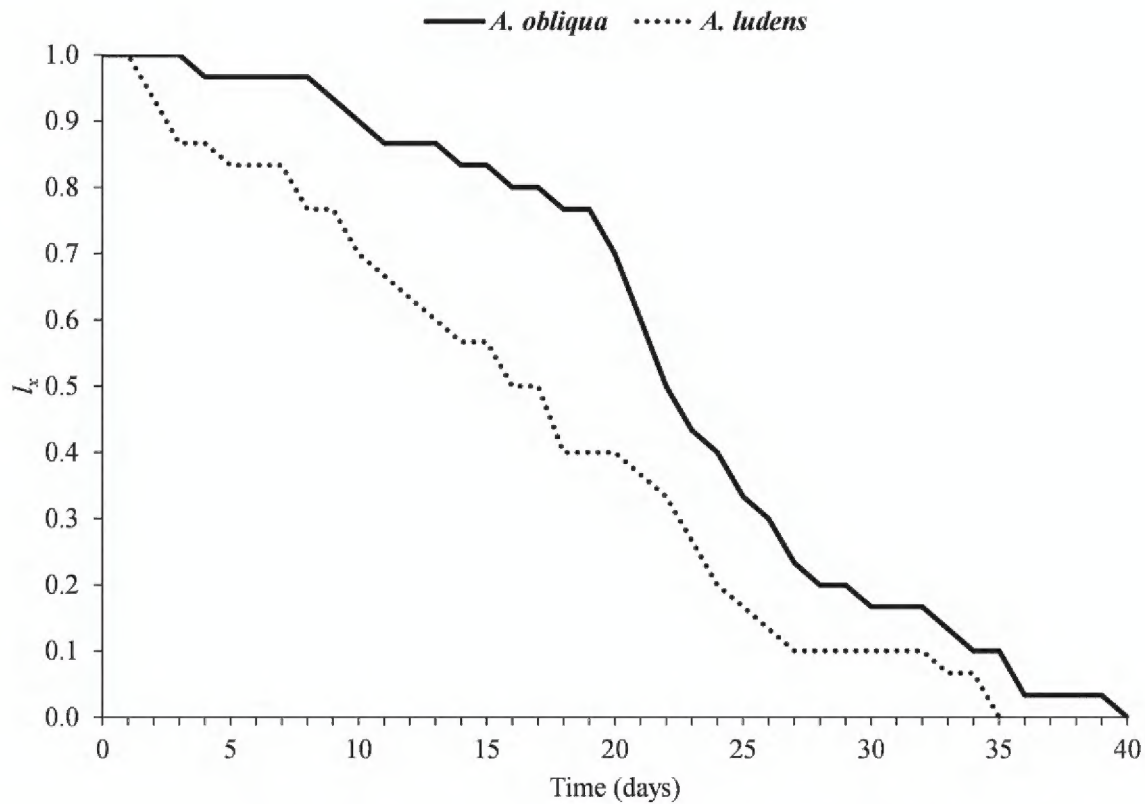
**Figure 3.** Daily percentage of parasitism of *U. anastrephae* in *A. obliqua* and *A. ludens* as hosts.

### Survival, reproduction, and population demographic parameters

Female survival was different (Log-Rank  $\chi^2 (1) = 4.6, p = .03$ ) between the two cohorts.

Females parasitizing *A. obliqua* larvae showed greater survival than those parasitizing *A. ludens* larvae with a mean longevity of  $22.93 \pm 8.37$  (mean  $\pm$  SD) and  $16.93 \pm 9.67$  days, respectively (Fig. 4). In both cohorts, males lived less than females, without statistically significant difference in their survival (Log-Rank  $\chi^2 (1) = 0.82, p = .4$ ). Males in the cohort with *A. obliqua* had a mean longevity of  $13.33 \pm 7.59$  days and  $15.63 \pm 7.22$  days with *A. ludens*.





**Figure 4.** Survival curves of *U. anastrephae* females parasitizing larvae of *A. obliqua* and *A. ludens* as hosts for the respective offspring development.

Reproductive rates were greater for parasitoids using *A. ludens* larvae as hosts than those using *A. obliqua*. The trajectories of net fecundity for both cohorts are shown in Fig. 5. Table 1 shows the gross and net fecundity rates, the daily mean of offspring production and the mean age for gross and net fecundity for the two cohorts. Regarding the population demographic parameters (Table 2), while the net reproductive rate ( $R_0$ ) was higher in *U. anastrephae* females that parasitized *A. ludens* larvae, all other population parameters were very similar for the two cohorts. The intrinsic rate of increase was similar ( $\approx 0.13$ ) between the two cohorts.

## Discussion

It was interesting to find that *U. anastrephae* could develop equally successfully in both hosts, one of them being its most frequent natural host (*A. obliqua*), and the other its host in the laboratory rearing colony (*A. ludens*). *Anastrepha ludens* has been reported as the natural host of *U. anastrephae* very rarely (Montoya et al. 2016). However, since most studies on natural parasitism of fruit fly parasitoids have generally been directed to the same fruits of specific interest (Aluja et al. 1990; López et al. 1999; García et al. 2020); it is possible that other fruits that have not been inspected are hosting *A. ludens* parasitized by *U. anastrephae*. Likewise, there may be confusion regarding the emergence of *U. anastrephae* from *A. obliqua* when it could also emerge from *A. ludens*, since parasitoids have been detected in mango, where both species of flies are present (Aluja et al. 1990). However, this assumption needs to be investigated.



**Table 1.** Reproductive parameters of *U. anastrephae* with larvae of *A. obliqua* and *A. ludens* as hosts.

Reproductive parameters	Host	
	<i>A. obliqua</i>	<i>A. ludens</i>
Gross fecundity rate	91.06	136.26
Net fecundity rate	47.50	62.61
Mean daily production	1.68	2.23
Mean age gross fecundity	28.90	30.37
Mean age net fecundity	28.41	28.84

**Table 2.** Population demographic parameters of *U. anastrephae* with larvae of *A. obliqua* and *A. ludens*.

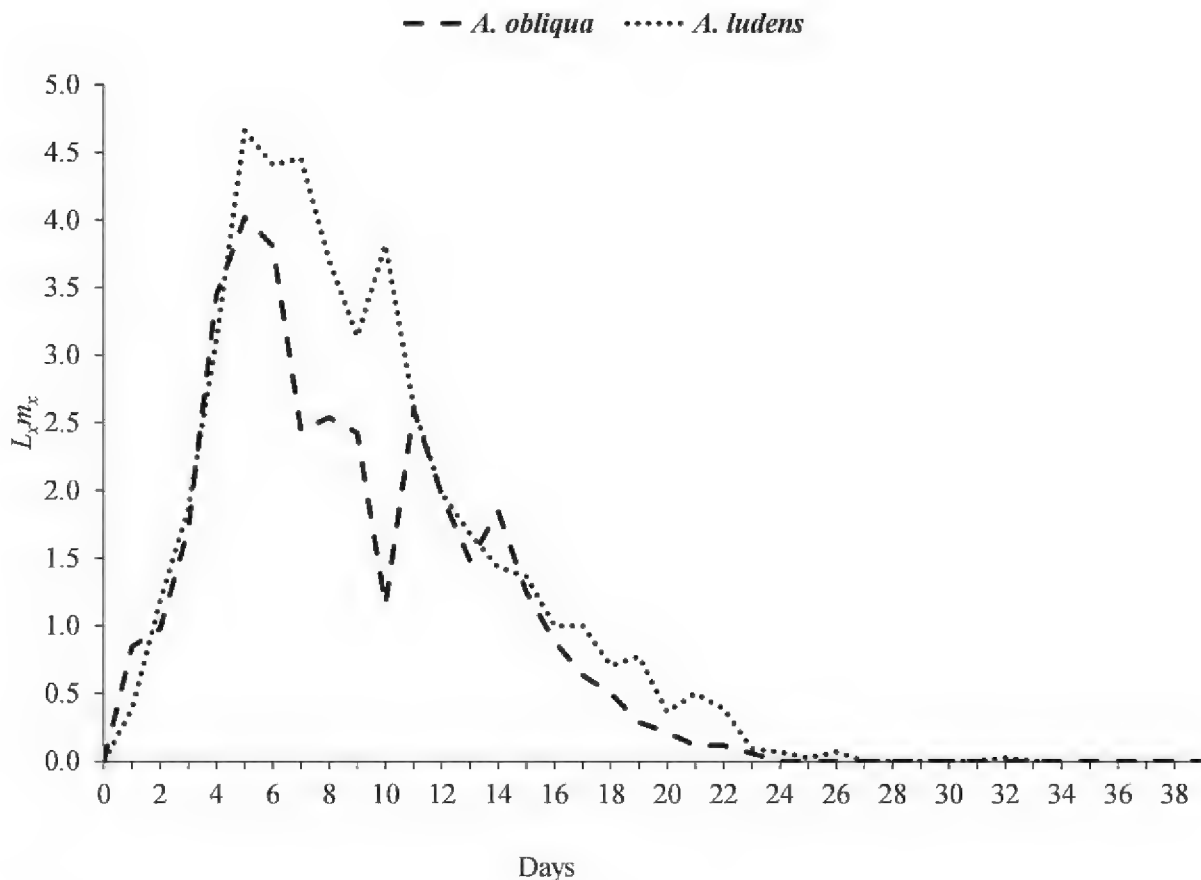
Population parameters	Host	
	<i>A. obliqua</i>	<i>A. ludens</i>
Net reproductive rate ( $R_0$ )	35.31	44.80
Mean generation time ( $T$ )	27.88	28.30
Intrinsic rate of increase ( $r$ )	0.128	0.134
Finite rate of increase ( $\lambda$ )	1.14	1.14
Doubling time ( $DT$ )	5.42	5.16
Adult life expectancy ( $e_x$ )	22.4	16.4

The higher reproductive rates found when *A. ludens* larvae were the host, compared to *A. obliqua*, can be attributed to three factors: 1) the effect of host switch, 2) the quality of the host, and/or 3) the immunological response. It is known that host switching may adversely affect the fitness of parasitoid species during the very first generations in a new host, although in subsequent generations their performance can improve (Zenil et al. 2004; Jones et al. 2015; Poncio et al. 2016). When the parasitoid *D. longicaudata* was previously maintained on *A. fraterculus* larvae, the adults parasitized more on this host than when *Ceratitis capitata* larvae (Wiedemann, 1824) were offered as an alternative host (Ovruski et al. 2011; Rohr et al. 2019). Something similar was observed with *Fopius arisanus* (Sonan, 1932) reared on *C. capitata* larvae for 28 generations. When adults were exposed to *Anastrepha* species larvae, the percentage of adult emergence was lower than in those exposed to *C. capitata* larvae (Zenil et al. 2004).

The use of alternative (factitious) hosts for parasitoid rearing has been an important technique (Pluke and Leibe 2006). When parasitoid colonization with the native host is a difficult, or expensive process, the use of this factitious host becomes an option (Boycheva et al. 2019). As mentioned above, *U. anastrephae* colonization with *A. obliqua* as host was an ineffective process. The use of *A. ludens* larvae as factitious host represented a good option.

Regarding the immune response of *A. obliqua* to parasitoids, it has been reported that its larva possesses 5–6 types of haemocytes that generate a strong immune response (phagocytosis and production of reactive oxygen species) (Silva et al. 2002; Gómez-Alonso et al. 2022). The presence of these haemocytes resulted in the melanization and encapsulation of the first immature stages of parasitoids (Silva et al. 2002; Cancino et al. 2022), which has not been observed in *A. ludens* (Poncio et al. 2016; Cancino et al.





**Figure 5.** Daily results of net maternity ( $L_x m_x$ ) of *U. anastrephae* with offspring daughters emerged from *A. obliqua* and *A. ludens*.

2020). This high immunity response of *A. obliqua* larva represents an important factor in increasing parasitoid mortality during development.

Host quality could be another factor. *Anastrepha ludens* larvae are larger in size than the *A. obliqua* ones. Under mass-rearing conditions, the mean pupal weight is 20 mg for *A. obliqua* and 24 mg for *A. ludens* (Orozco-Dávila et al. 2017). Usually, larger size hosts are preferred by parasitoids, showing an increase in their fecundity (Brodeur and Boivin 2004; Cohen et al. 2005; Gao et al. 2016). Another reason may be the better adaptation and more stability of *A. ludens* to mass rearing conditions. Compared with *A. obliqua*, it has been, easier to colonize and maintain under laboratory conditions (Orozco-Dávila et al. 2017; Aceituno-Medina et al. 2020).

The lower survival of the parasitoids exposed to *A. ludens* larvae can be explained by the cost of reproduction, the higher the fecundity, the lower the longevity. Since the net reproductive rate and the intrinsic rate of increase were higher for parasitoids reared on *A. ludens* than those reared on *A. obliqua* (Table 2), this trade-off can be considered convenient in terms of fitness.

The demographic parameters we found here were like those reported by Vargas et al (2002) with other larval-pupal braconid endoparasitoid reared on different hosts. For example, the intrinsic rate of increase for *D. longicaudata* and *Psytalia incisi* (Silvestri, 1916) was  $r = 0.12$  and  $0.10$ , respectively, both reared on *Bactrocera dorsalis* larvae (Hendell, 1912). This suggests that *U. anastrephae* has the potential to be used as a biocontrol agent, as it has growth rates like other parasitoid species that have been used for the control of fruit flies.



The intrinsic growth rate we found here with *A. ludens* as a host ( $r = 0.134$ ) was 2-fold greater than that reported by Aluja et al. (2009) using the same host when they were colonizing this species for laboratory rearing ( $r = 0.079$ ). This means that the *U. anastrephae* strain tested here has adapted to this alternative host species, and it can be used for mass production. The sex ratio is a fundamental aspect for biological control, since the females are the ones that attack the host and contribute to population growth. A female-biased sex ratio would be most desirable (Montoya et al. 2013; Nurkomar et al. 2021). Here we found that the sex ratio was female-biased, about 70% female ( $\approx 3:1$ ) for both hosts used. This proportion coincides with that obtained by Poncio et al. (2018), with a percentage of 65% using *A. obliqua* larvae as hosts. This proportion is adequate for the purposes of augmentative biological control.

The reason why under natural conditions *U. anastrephae* is commonly associated to *A. obliqua* could be the size of the fruit species used by the fruit fly species (Hernández-Ortíz et al. 1994; López et al. 1999). *Utetes anastrephae* has a short ovipositor that might be strongly adapted to small fruits. In general, *A. obliqua* infest fruits that are smaller in size (*Spondias* spp., *Psidium guajava* L.) than those commonly infested by *A. ludens* (*Citrus* spp., *Casimiroa edulis* La Llave & Lex). Then, in large fruits the host larvae might be out of reach for *U. anastrephae*. Also, semiochemicals emitted by fruits infested by *A. obliqua* (usually small) can determine this preference (Aluja et al. 2013). Another possibility, derived from our results, will be to use *A. obliqua* as a host for several generations, expecting that reproductive and population parameters could increase. However, the greater difficulty and cost of producing *A. obliqua* should be considered.

This demographic analysis of *U. anastrephae* comparing two hosts indicates that *A. ludens* can be used as a suitable host for mass production, although releases of parasitoids be strategically targeted to control *A. obliqua*. Biological control of *A. obliqua* in non-commercial hosts could be a strategy to prevent the movement of populations from these hosts to fruit orchards (i.e., mango orchards), where fruits are grown for commercial purpose (Cancino et al. 2019b; Montoya et al. 2000). *Anastrepha obliqua* is a major pest of mango in the Americas and is highly desirable to have a biocontrol alternative to minimize its damage (Cancino et al. 2019b; Ruiz-Arce et al. 2019).

The information generated here can be useful for decision making on the use of native parasitoids in augmentative biological control and new proposals to complement or improve current strategies for managing *Anastrepha* fruit flies. It would be interesting to know the behaviour of *U. anastrephae* reared in *A. ludens* larvae, on host preference in the presence of these two host species studied here, both in the laboratory and under field conditions.

## Conclusion

This study provides information about the potential use of the native parasitoid *U. anastrephae* in augmentative biocontrol programs against *A. obliqua* fruit flies. Our results show that both, *A. obliqua* and *A. ludens* larvae can be used as hosts for mass



rearing purposes. Although *A. ludens* is not a common natural host, it can be used as a factitious host, considering the higher fecundity rate observed and considering that *A. ludens* is easier to mass produce than *A. obliqua* (Orozco-Dávila et al. 2017).

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## References

- Aceituno-Medina M, Rivera-Ciprian JP, Hernández E (2020) Evaluation of a pelleted diet for larval mass-rearing of *Anastrepha ludens* and *Anastrepha obliqua*. *Entomologia Experimentalis et Applicata* 168: 502–512. <https://doi.org/10.1111/eea.12903>
- Aluja M, Guillen J, Liedo P, Cabrera P, Rios E, De la Rosa G, Celedonio H, Mota D (1990) Fruit infesting tephritids (Dipt.: Tephritidae) and associated parasitoids in Chiapas, México. *Entomophaga* 35: 39–48. <https://doi.org/10.1007/BF02374299>
- Aluja M, Sivinski J, Ovruski S, Guillén L, López M, Cancino J, Torres-Anaya A, Gallegos-Chan G, Ruíz L (2009) Colonization and domestication of seven species of native New World hymenopterous larval-prepupal and pupal fruit fly (Diptera: Tephritidae) parasitoids. *Biocontrol Science and Technology* 19: 49–79. <https://doi.org/10.1080/09583150802377373>
- Aluja M, Ovruski SM, Sivinski J, Córdova-García G, Schliserman P, Núñez-Campero SR, Ordano M (2013) Inter-specific competition and competition-tree space in the tephritid parasitoids *Utetes anastrephae* and *Doryctobracon areolatus* (Hymenoptera: Braconidae: Opiinae). *Ecological Entomology* 38: 485–496. <https://doi.org/10.1111/een.12039>
- Ayala A, Pérez-Lachaud G, Toledo J, Liedo P, Montoya P (2018) Host acceptance by three native braconid parasitoid species attacking larvae of the Mexican fruit fly, *Anastrepha ludens* (Diptera, Tephritidae). *Journal Hymenoptera Research* 63: 33–49. <https://doi.org/10.3897/jhr.63.23724>
- Bellows Jr TS, Van Driesche RG, Elkinton JS (1992) Life-table construction and analysis in the evaluation of natural enemies. *Annual Review of Entomology* 37: 587–614. <https://doi.org/10.1146/annurev.en.37.010192.003103>
- Boycheva SW, Romeis J, Collatz J (2019) Influence of the rearing host on biological parameters of *Trichopria drosophilae*, a potential biological control agent of *Drosophila suzukii*. *Insects* 10(6): 183. <https://doi.org/10.3390/insects10060183>
- Brodeur J, Boivin G (2004) Functional ecology of immature parasitoids. *Annual Review of Entomology* 49: 27–49. <https://doi.org/10.1146/annurev.ento.49.061703.153618>



- Cancino J, Ruíz L, Sivinski J, Gálvez FO, Aluja M (2009) Rearing of five hymenopterous larval-prepupal (Braconidae, Figitidae) and three pupal (Diapriidae, Chalcidoidea, Eurytomidae) native parasitoids of the genus *Anastrepha* (Diptera: Tephritidae) on irradiated *A. ludens* larvae and pupae. *Biocontrol Science and Technology* 19: 193–209. <https://doi.org/10.1080/09583150802377423>
- Cancino J, Ruíz L, López E, Aguilar E, Gálvez C, Montoya P, Liedo P (2019a) Suppression of *Ceratitis capitata* (Wied.) (Diptera: Tephritidae) populations in coffee in the Mexico-Guatemala border region through the augmentative releases of *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae). *Biocontrol Science and Technology* 29(8): 822–826. <https://doi.org/10.1080/09583157.2019.1608507>
- Cancino, J, Bello-Rivera A, Cárdenas-Lozano J, Gálvez-Cárdenas F, García-Pérez V, Camacho-Bojórquez E, Segura-Bailon E, Leyva-Castro M, Ramírez y Ramírez F (2019b) Biological control of *Anastrepha* populations in wild areas to strengthen the commercial status of mango production along the pacific coast of Mexico. In: Pérez-Staples D, Díaz-Fleischer DE, Montoya P, Vera MT (Eds) *Area-wide management of fruit fly pests*. CRC Press (Boca Raton, FL, USA), 235–249. <https://doi.org/10.1201/9780429355738>
- Cancino J, Ruíz L, López P, Moreno FM (2020) Cría masiva de parasitoides. In: Montoya P, Toledo J, Hernández E (Eds) *Moscas de la fruta: Fundamentos y procedimientos para su manejo*. S y G editores (Ciudad de México), 463–481.
- Cancino J, Ayala A, Ríos L, López P, Suárez L, Ovruski SM, Hendrichs J (2022) Increasing radiation doses in *Anastrepha obliqua* (Diptera: Tephritidae) larvae improve parasitoid mass-rearing attributes. *Bulletin of Entomological Research*: 1–11. <https://doi.org/10.1017/S0007485322000219>
- Carey JR (1993) *Applied demography for biologists with special emphasis on insects*. Oxford University Press, New York, 206 pp.
- Carey JR, Roach DA (2020) *Biodemography: An introduction to concepts and methods*. Princeton University Press, New Jersey, 480 pp. <https://doi.org/10.2307/j.ctvkjb4n8>
- Cohen JE, Jonsson T, Müller CB, Godfray HC, Savage VM (2005) Body sizes of hosts and parasitoids in individual feeding relationships. *Proceedings of the National Academy of Sciences of the United States of America* 102(3): 684–689. <https://doi.org/10.1073/pnas.0408780102>
- Eitam A, Holler T, Sivinski J, Aluja M (2003) Use of host fruit chemical cues for laboratory rearing of *Doryctobracon areolatus* (Hymenoptera: Braconidae), a parasitoid of *Anastrepha* spp. (Diptera: Tephritidae). *Florida Entomologist* 86(2): 211–216. [https://doi.org/10.1653/0015-4040\(2003\)086\[0211:UOHFCC\]2.0.CO;2](https://doi.org/10.1653/0015-4040(2003)086[0211:UOHFCC]2.0.CO;2)
- Fernandes EC, Souza MM, Nava DE, Silva JG, Araujo EL (2021) Fertility life table and biology of *Tetrastichus giffardianus* (Hymenoptera: Eulophidae) in the larvae of *Ceratitis capitata* (Diptera: Tephritidae). *Bulletin of Entomological Research* 111: 182–189. <https://doi.org/10.1017/S0007485320000498>
- Ganjisaffar F, Perring TM (2020) Life history evaluation of *Ooencyrtus lucidus*, a newly described egg parasitoid of *Bagrada hilaris*. *Insects* 11(5): e292. [14 pp] <https://doi.org/10.3390/insects11050292>



- Gao S, Tang Y, Wei K, Wang X, Yang Z, Zhang Y (2016) Relationships between body size and parasitic fitness and offspring performance of *Sclerodermus pupariae* Yang et Yao (Hymenoptera: Bethyridae). PLoS ONE 11(7): e0156831. <https://doi.org/10.1371/journal.pone.0156831>
- García FRM, Ovruski SM, Suárez L, Cancino J (2020) Biological control of tephritid fruit flies in the Americas and Hawaii: A review of the use of parasitoids and predators. Insects 11(10): e662. [34 pp] <https://doi.org/10.3390/insects11100662>
- Gómez-Alonso I, Baltierra-Urbe S, Sánchez-Torres L, Cancino-Díaz M, Cancino-Díaz J, Rodríguez-Martínez S, Ovruski SM, Hendrichs J, Cancino J (2022) Irradiation and parasitism affect the ability of larval hemocytes of *Anastrepha obliqua* for phagocytosis and the production of reactive oxygen species. Archives of Insect Biochemistry and Physiology [Early view] e21953. <https://doi.org/10.1002/arch.21953>
- Gonçalves SR, Nunes AM, Poncio S, Manica-Berto R, Nörnberg SD, Grützmacher AD, Nava DE (2018) Bionomics, thermal requirements and life table of the fruit fly parasitoid *Doryctobracon areolatus* (Hymenoptera: Braconidae) under various thermal regimes. Biological Control 127: 101–108. <https://doi.org/10.1016/j.biocontrol.2018.08.025>
- Gowda GB, Pandi GGP, Ullah F, Patil NB, Sahu M, Adak T, Pokhare S, Yadav MK, Mahendiran A, Mittapelly P, Desneux N, Rath PC (2021) Performance of *Trichogramma japonicum* under field conditions as a function of the factitious host species used for mass rearing. PLoS ONE 16(8): e0256246. <https://doi.org/10.1371/journal.pone.0256246>
- Hernández-Ortíz V, Pérez-Alonso R, Wharton RA (1994) Native parasitoids associated with the genus *Anastrepha* (Dipt.: Tephritidae) in los Tuxtlas, Veracruz, México. Entomophaga 39(2): 171–178. <https://doi.org/10.1007/BF02372355>
- Iranipour S, Vaez N, Ghanbalani GN, Zakaria RA, Jafarloo MM (2010) Effect of host change on demographic fitness of the parasitoid, *Trichogramma brassicae*. Journal of Insect Science 10: 78. <https://doi.org/10.1673/031.010.7801>
- Jervis MA, Copland MJW (1996) The life cycle. In: Jervis MA, Kidd N (Eds) Insect natural enemies: Practical approaches to their study and evaluation. Chapman & Hall (London), 148–154. [https://doi.org/10.1007/978-94-011-0013-7\\_2](https://doi.org/10.1007/978-94-011-0013-7_2)
- Jones TS, Bilton AR, Lorraine M, Sait SM (2015) Host switching in a generalist parasitoid: Contrasting transient and transgenerational costs associated with novel and original host species. Ecology and Evolution 5(2): 459–465. <https://doi.org/10.1002/ece3.1333>
- López M, Aluja M, Sivinski J (1999) Hymenopterous larval-pupal and pupal parasitoids of *Anastrepha* flies (Diptera: Tephritidae) in Mexico. Biological Control 15: 119–129. <https://doi.org/10.1006/bcon.1999.0711>
- Montoya P, Liedo P, Benrey B, Cancino J, Barrera JF, Sivinski J, Aluja M (2000) Biological control of *Anastrepha* spp. (Diptera: Tephritidae) in mango orchards through augmentative releases of *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae). Biological Control 18: 21–224. <https://doi.org/10.1006/bcon.2000.0819>
- Montoya P, Cancino J, Zenil M, Santiago G, Gutiérrez JM (2007) The augmentative biological control component in the Mexican National Campaign against *Anastrepha* spp. fruit flies. In: Vreysen MJB, Robinson AS, Hendrichs J (Eds) Area-wide control of insect pests:



- From research to field implementation. Springer (Netherlands): 661–670. [https://doi.org/10.1007/978-1-4020-6059-5\\_61](https://doi.org/10.1007/978-1-4020-6059-5_61)
- Montoya P, Ruíz L, Pérez-Lachaud, Cancino J, Liedo P (2013) Field superparasitism by *Diachasmimorpha longicaudata* attacking *Anastrepha* spp. larva on mango fruits. *Biological Control* 64: 160–165. <https://doi.org/10.1016/j.biocontrol.2012.10.015>
- Montoya P, Ayala A, López P, Cancino J, Cabrera H, Cruz J, Martínez AM, Figueroa I, Liedo P (2016) Natural parasitism in fruit fly (Diptera: Tephritidae) populations in disturbed areas adjacent commercial mango orchards in Chiapas and Veracruz, Mexico. *Environmental Entomology* 45: 328–337. <https://doi.org/10.1093/ee/nvw001>
- Murillo FD, Cabrera-Mireles H, Barrera JF, Liedo P, Montoya P (2018) Intrinsic competition between resident and invasive parasitoids (Hymenoptera: Braconidae) that attack the West Indian fruit fly *Anastrepha obliqua* under field conditions. *Biocontrol Science and Technology* 29(3): 1–11. <https://doi.org/10.1080/09583157.2018.1548573>
- Núñez-Campero SR, Aluja M, Rull J, Ovruski SM (2014) Comparative demography of three neotropical larval-prepupal parasitoid species associated with *Anastrepha fraterculus* (Diptera: Tephritidae). *Biological Control* 69: 8–17. <https://doi.org/10.1016/j.biocontrol.2013.10.013>
- Nurkomar I, Azhar A, Damayanti B (2021) Sex allocation and field population sex ratio of *Apanteles taragamae* Viereck (Hymenoptera: Braconidae), a larval parasitoid of the cucumber moth *Diaphania indica* Saunders (Lepidoptera: Crambidae). *Open Agriculture* 6: 673–681. <https://doi.org/10.1515/opag-2021-0045>
- Orozco-Dávila D, Quintero L, Hernández E, Solís E, Artiaga T, Hernández R, Ortega C, Montoya P (2017) Mass rearing and sterile insect releases for the control of *Anastrepha* spp. pests in Mexico-A review. *Entomologia Experimentalis et Applicata* 164(3): 176–187. <https://doi.org/10.1111/eea.12581>
- Ovruski S, Aluja M, Sivinski J, Wharton R (2000) Hymenopteran parasitoids on fruit-infesting Tephritidae (Diptera) in Latin America and the southern United States: Diversity, distribution, taxonomic status and their use in fruit fly biological control. *Integrated Pest Management Reviews* 5: 81–107. <https://doi.org/10.1023/A:1009652431251>
- Ovruski SM, Bezdjian LP, Van Nieuwenhove GA, Albornoz-Medina P, Schliserman P (2011) Host preference by *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae) reared on larvae of *Anastrepha fraterculus* and *Ceratitis capitata* (Diptera: Tephritidae). *Florida Entomologist* 94(2): 195–200. <https://doi.org/10.1653/024.094.0211>
- Pluke RWH, Leibe GL (2006) Host preferences of *Trichogramma pretiosum* and the influence of prior ovipositional experience on the parasitism of *Plutella xylostella* and *Pseudoplusia includens* eggs. *Biocontrol* 51: 569–583. <https://doi.org/10.1007/s10526-005-1033-3>
- Poncio S, Montoya P, Cancino J, Nava DE (2016) Is *Anastrepha obliqua* (Diptera: Tephritidae) a natural host of the Neotropical parasitoids *Doryctobracon crawfordi* and *Opius hirtus*? *Austral Entomology* 55(1): 18–24. <https://doi.org/10.1111/aen.12146>
- Poncio S, Montoya P, Cancino J, Nava DE (2018) Best host age of *Anastrepha obliqua* (Diptera: Tephritidae) for multiplication of four native parasitoids from the Americas. *Journal of Insect Science* 18(2): e36. [8 pp] <https://doi.org/10.1093/jisesa/iey023>



- Rohr RA, Jahnke SM, Redaelli LR (2019) Influence of the original host in the preference of *Aganaspis pelleranoi* and *Doryctobracon areolatus*, parasitoids of Tephritidae larvae. Bulletin of Insectology 72: 13–20. [Retrieved from:] <http://www.bulletinofinsectology.org/pdfarticles/vol72-2019-013-020rohr.pdf>
- Ruiz-Arce R, Islam Md-S, Aluja M, McPheron BA (2019) Genetic variation in *Anastrepha obliqua* (Diptera: Tephritidae) in a highly diverse tropical environment in the Mexican state of Veracruz. Journal of Economic Entomology 112(6): 2952–2965. <https://doi.org/10.1093/jee/toz223>
- R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>
- Silva JEB, Boleli IC, Simões ZLP (2002) Hemocyte types and total and differential counts in unparasitied and parasitized *Anastrepha obliqua* (Diptera, Tephritidae) larvae. Brazilian Journal of Biology 62(4A): 689–699. <https://doi.org/10.1590/s1519-69842002000400017>
- Stark JD, Banks JE, Acheampong S (2004) Estimating susceptibility of biological control agents to pesticides: Influence of life history strategies and population structure. Biological Control 29: 392–398. <https://doi.org/10.1016/j.biocontrol.2003.07.003>
- Vargas RI, Ramadan M, Hussain T, Mochizuki N, Bautista RC, Stark JD (2002) Comparative demography of six fruit fly (Diptera: Tephritidae) parasitoids (Hymenoptera: Braconidae). Biological Control 25: 30–40. [https://doi.org/10.1016/S1049-9644\(02\)00046-4](https://doi.org/10.1016/S1049-9644(02)00046-4)
- Zenil, M, Liedo P, Williams T, Valle J, Cancino J, Montoya P (2004) Reproductive biology of *Fopius arisanus* (Hymenoptera: Braconidae) on *Ceratitis capitata* and *Anastrepha* spp. (Diptera: Tephritidae). Biological Control 29(2): 169–178. [https://doi.org/10.1016/S1049-9644\(03\)00140-3](https://doi.org/10.1016/S1049-9644(03)00140-3)